

REVIEW AND
SYNTHESIS

Ecosystem engineering in space and time

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Abstract

The ecosystem engineering concept focuses on how organisms physically change the abiotic environment and how this feeds back to the biota. While the concept was formally introduced a little more than 10 years ago, the underpinning of the concept can be traced back to more than a century to the early work of Darwin. The formal application of the idea is yielding new insights into the role of species in ecosystems and many other areas of basic and applied ecology. Here we focus on how temporal, spatial and organizational scales usefully inform the roles played by ecosystem engineers and their incorporation into broader ecological contexts. Two particular, distinguishing features of ecosystem engineers are that they affect the physical space in which other species live and their direct effects can last longer than the lifetime of the organism – engineering can in essence outlive the engineer. Together, these factors identify critical considerations that need to be included in models, experimental and observational work. The ecosystem engineering concept holds particular promise in the area of ecological applications, where influence over abiotic variables and their consequent effects on biotic communities may facilitate ecological restoration and counterbalance anthropogenic influences.

Keywords

Abiotic factors, models, restoration.

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INTRODUCTION

One major goal of ecology is to understand the distribution and abundance of species based on how organisms interact with other individuals and their environment. Throughout the history of ecology, the importance of both abiotic and biotic interactions has been recognized. Yet, as the first paper formally introducing the concept of ecosystem engineers suggested (Jones *et al.* 1994), a deeper understanding of many systems can be obtained when specific

organismal interactions with the physical environment are broken out and emphasized. Such recognition has a long tradition pre-dating the term ‘ecosystem engineer’ (Table 1), and conceptual papers (Jones *et al.* 1994, 1997) have catalysed much recent research (see overview in Wright & Jones 2006). Nevertheless, we posit that much more use could be made of the concept in both basic and applied ecology, and present ways to do so.

Our central theme is the importance of time and space scales as a key to understanding the importance of and use

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of the ecosystem engineering concept. As some critics of the concept have noted (e.g. Reichman & Seabloom 2002), all organisms affect (and are affected by) their physical environment. So the utility of the ecosystem engineering concept depends on knowing when the modification of the environment by an organism has to be explicitly considered, rather than simply absorbed as part of the description of direct interactions between organisms. Explicit inclusion of engineering is clearly required when the temporal and spatial scales of engineering effects differ from the temporal and spatial scales of direct organismal interactions (see Fig. 1). This is an operational, rather than a conceptual view, and not all interactions classified as ecosystem engineering by others (Jones *et al.* 1994; Wright & Jones 2006), would meet this scale test. Here we take a pragmatic view, and focus on elucidating cases where explicit inclusion of the interactions of ecosystem engineering changes our predictions and understanding, rather than identifying ecosystem engineering from first principles. Thus we are not studying all aspects of ecosystem engineering, but are instead focusing on a subset of all ecosystem engineering that we argue is of particular importance.

The goals of the current study are to: (i) illustrate how understanding the dynamics and effects of ecosystem engineers is enhanced by the use of temporal and spatial scales as an underlying concept; (ii) emphasize that there are important cases where understanding scale-dependent changes in processes or interactions requires explicit inclusion of engineering; and (iii) demonstrate how the unique modification of space by ecosystem engineers informs more general ecological thinking. Some engineering organisms cause large, structurally mediated physical mod-

ifications to their environment that persist on time scales longer than their individual lifetimes, and with impacts at much larger spatial scales than the organism itself. Naturally, interactions over shorter and smaller scales also occur, and cannot be ignored. As all organisms can have some effect on physical aspects of the environment, the importance of ecosystem engineering is therefore a matter of degree and scale. A focus on scales (Levin 1992) helps us understand the dynamics of the engineering species and their effects while contributing to our fundamental understanding of ecosystems.

We begin with an overview of the importance of temporal and spatial considerations in understanding ecosystem engineering, before reviewing the current state of models of ecosystem engineers. This review naturally leads to an examination of experimental and observational approaches at various levels of organization that take into account time and space scales when using the ecosystem engineering concept. We then point out the utility of the concept in applied ecology, where it may help meet challenges in restoration (Byers *et al.* 2006) and other areas. Despite the growing interest in and development of the ecosystem engineering concept, many challenges remain, and we conclude with a brief perspective on future directions.

TEMPORAL AND SPATIAL SCALES OF ENGINEERING AND BIOTIC-BIOTIC INTERACTIONS

Previous reviews have demonstrated that ecosystem engineering is widespread (Wright & Jones 2006) and that there has been a long history of studying the process (Table 1).

Table 1 Selected, significant studies in the development and use of the ecosystem engineering concept

Reference	Subject	Significance
Darwin (1881)	Earthworms	Classic early example of ecosystem engineering
Shaler (1892)	Soil processes	Early, comprehensive review of plant and animal effects (engineering) on soil processes
Varga (1928)	Phytotelomata	Recognition that plants create habitats for other organisms
Clements (1916)	Succession	Plants can alter environmental (abiotic) conditions such that they may no longer benefit themselves
Shreve (1931)	Nurse plants	Facilitation by plant engineering
Dayton (1972)	Foundation species	Organisms build the structure of the environment
Meadows & Meadows (1991)	Burrowing animals and bioturbation	Broad coverage of animal soil/sediment influences
Naiman (1988)	Large animal effects on ecosystems	Species and ecosystem effects largely through ecosystem engineering
Jones <i>et al.</i> (1994, 1997)	Ecosystem engineering as a conceptual tool	Formalized the concept of ecosystem engineering
Gurney & Lawton (1996)	Model of ecosystem engineer	First explicit dynamic ecosystem engineering population model
Laland <i>et al.</i> (1999)	Niche construction	Two-locus general evolutionary model of ecosystem engineering
Wilby <i>et al.</i> (2001)	Ants	Integrated engineering and trophic roles of species

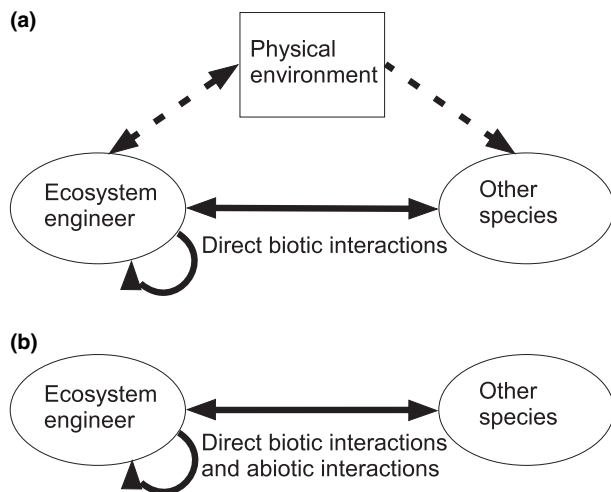


Figure 1 Diagrammatic representation of interactions of ecosystem engineers. In part (a) the physical environment is explicitly included, while in part (b) the engineering effects are included only implicitly along with direct biotic interactions. The dashed lines represent the abiotic interactions. The explicit inclusion of the engineering process separately from the biotic processes as depicted in (a) is required when the spatial scale of the engineering effects is broader than the scale of biotic effects or the effects of engineers last longer than biotic effects so a different temporal scale is needed.

Although the concept can be useful in elucidating different kinds of ecological interactions and consequences, the full significance of the ecosystem engineering concept is manifested in how engineer impacts differ from biotic interactions. We use time and space scales to demonstrate how ecosystem engineering has different consequences than would arise from purely biotic interactions, showing both how and why to incorporate ecosystem engineering into ecological theory.

Temporal scales

Interspecific interactions, both with and without modifications to the physical environment (i.e. engineering vs. non-engineering), can occur on time scales from the infinitesimally small to the extraordinarily protracted. Engineering activities such as the creation of transient bubble nets by cetaceans and intertidal feeding pits by rays can have longevities of seconds to hours (Table 2), operating on time scales comparable with (or shorter than) the imposition and resultant effects of biotic–biotic interactions such as prey consumption and exploitative competition. Non-engineering activities also can have effects that are essentially permanent, such as the extinction of species caused by over-predation. However, we argue that on the whole, engineering is more likely to have long-term effects than non-engineering.

A legacy effect of an ecosystem engineer is the persistence of engineered aspects of the environment and the direct effects that stem from this after the engineer is dead or absent. This is clearly a category that resides on different time scales than biotic effects. Because autogenic engineers, by definition (Jones *et al.* 1994), change the environment via their own physical structure, the longevity of an engineering effect of an autogenic engineer after its death is dependent upon the persistence of its remains (e.g. reef building, Lenihan 1999). In fact, the physical structures of autogenic engineers like trees and coral often persist long after the organism's death (Table 2).

Allogenic engineers change living or non-living materials in the environment from one physical state to another (Jones *et al.* 1994), invariably resulting in legacy, albeit of variable duration. Many allogenic engineering effects are dependent on the vitality of the engineer for constant maintenance and upkeep, e.g. tents built by tent caterpillars. However, the consequences of allogenic engineering can persist for long times. A classic extended legacy example is a beaver dam. Wright *et al.* (2003) report that beaver are active at a site for *c.* 4 years (range: 1–20). After the dam is abandoned some disintegration and drainage occurs forming a beaver meadow. These meadows can persist for over 70 years and rarely convert back into the original forested riparian zone. Thus, explicit inclusion of the time scale will be required, and the physical structure operates essentially independently of the engineering organism.

In other cases the feedback between engineer and structure, and thus the temporal legacy of the engineering, is ongoing and more complex. Villenave *et al.* (1999) present an interesting example where a legacy was only apparent following interaction with human disturbance. The authors examined plots with and without earthworms on tilled and untilled soil. In the untilled soil, no difference in soil organic matter was observed regardless of the presence of worms. However, in tilled soil, plots with worms had higher soil organic matter after 3 years. Tilling apparently dispersed macro-aggregate structures (which often protect organic matter from mineralization), and the worms re-aggregated them. In no-tilled land, it appeared that the conservation of macro-aggregate structures inherited from past earthworms had hidden the present effect of worms.

Just as the concept of exponential growth leads to understanding density dependence and limits to growth, inclusion of ecosystem engineering necessarily leads to the important question of what limits the effect of engineering. In some cases, the limit to engineering may be easy to identify because the scale of feedback is short. Flecker *et al.* (1999) demonstrate that tropical tadpoles can act as ecosystem engineers by reducing sediment accrual rates; the resulting low availability of sediment can negatively feedback on tadpoles by reducing their daily growth rates. A

Table 2 Examples illustrating how ecosystem engineers create structures that can operate on temporal scales and larger spatial scales that differ from direct biotic interactions

Taxa	Group or common name	Habitat	Structure	Auto/allogeneic	Size of engineered patch (m ²)	Persistence (years)	Reference
<i>Martiodrilus cariniguensis</i>	Earthworm	Tropical savanna	Soil casts	Allo	0.02	0.2–0.9	Decaëns (2000)
<i>Microhodotermes viator</i>	Termite	Savanna	Mounds	Allo	152–224	4000	Moore & Pickett (1991)
<i>Macrotermes bellicosus</i>	Termite	Savanna/woodland	Mounds	Allo	4.9–5.7	20–25	Lepage (1984)
<i>Castor canadensis</i>	Beaver	NE forest	Dam-pond–meadow complex	Allo	Depends on topography	4.8 (time occupancy of site); 70 (recovery of abandoned sites)	Wright <i>et al.</i> (2004)
<i>Pseudaletia</i> spp.	Lepidopteran	Oak woodland	Leaf ties	Allo	0.01	0.11–0.15	Lill & Marquis (2003)
<i>Calacarus flagelliveta</i>	Eriophysis mite	Tropical agro-forest	Leaf ties	Allo	0.002	0.33–0.5	Fournier <i>et al.</i> (2003)
<i>Hystrix indica</i>	Desert porcupine	Negev desert	Soil pits	Allo	0.0257	20	Shachak <i>et al.</i> (1991)
<i>Megaptera novaeangliae</i>	Humpback whale	Pelagic	Bubble nets	Allo	7–707	3.90 × 10 ⁻⁶	Sharpe (1984)
<i>Mya arenaria</i>	Soft shell clam	Intertidal	Shell beds	Auto	15 680 000	100	Palacios <i>et al.</i> (2000)
Many species (corals, bryozoans, molluscs, etc.)	Hardparts of many taxa	Intertidal/subtidal	Shell beds	Auto	Various	500 million	Kidwell (1986)
<i>Spartina anglica</i>	Cordgrass	Intertidal	Sediment hummocks	Auto	20–5000(?)	3–20	McGrorty & Goss-Custard (1987)
<i>Thomomys bottae</i>	Gopher	Grassland	Mounds	Allo	707–2000	A few years	Wu & Levin (1994)
<i>Dipodomys spectabilis</i>	Kangaroo rat	Desert	Mounds	Allo	7–20	Several decades	Guo (1996)
Several species	Tropical trees	Neotropical forest	Woody habitat	Auto	0.00049–0.1	10	Lang & Knight (1979)
<i>Abies balsamea</i>	Balsam fir	Conifer forest	Woody habitat	Auto	0.03	100	Lambert <i>et al.</i> (1980)
Several species	Tropical trees	Neotropical forest	Leaf litter	Auto	0.31–10.78	0.62	La Caro & Rudd (1985)
Centrarchidae	Sunfish	Temperate lake	Nests	Allo	0.28–1.22	1	Thorp (1988)
Dasyatid ray	Stingray	Intertidal	Pits	Allo	0.07–0.5	0.003–0.01	D'Andrea <i>et al.</i> (2002)

Each case is classified as autogenic or allogenic (as defined in the text). Note that not all of these do operate on longer or larger scales, but many do and it is such cases that are the focus of this article.

more puzzling example is in Lenihan (1999), who showed that oysters on subtidal reef crests survive best by avoiding sedimentation and grow fastest due to faster water flow bringing a greater flux of food. Oyster recruitment was fairly similar over all parts of the reef. Thus reef growth would seemingly be fastest at the crest, but many reefs stop growing far short of the top of water, so there must be some other limit to this engineering effect. As this example shows, the limits to engineering often lie outside the realm of what investigators usually study (see Gutiérrez *et al.* 2003 for a review of mollusk feedbacks).

Spatial scales

Ecosystem engineers can have dramatic effects at both large and small spatial scales, where scale is defined relative to the engineer. Although non-engineering activities can occur at relatively large spatial scales, such as trophic flows across connecting but discrete habitats (e.g. Talley *et al.* 2006), there is a widespread appreciation that an important aspect of engineering when compared with biotic interactions is that physical modifications influence processes at large spatial scales (Fig. 1). The tendency to think of engineers as only having large-scale effects, however, may reflect scientists' conservative (and erroneous) tendency to only label large, dramatic effects as ecosystem engineering (and similarly, to think that ecosystem engineering implies large scale rather than the biotic–abiotic–biotic coupling). The impression that large-scale effects predominate may also be driven by the larger spatial impact of the most commonly studied engineers, e.g. beaver, kelp and coral reefs. A more holistic view of engineers across a broad size and activity spectrum may produce a more balanced consensus as to the scale of their effects. For example, Lavelle (2002) reviews soil engineers (ants, termites and earthworms) and demonstrates that many of their effects are fine scale.

As shown in Table 2, the scales of engineering include and go beyond the scales of biotic processes, and all the scales need to be considered (Fig. 1). However, as we emphasize here the smaller scales are much more difficult to study and may have less dramatic effects. Moreover, processes at different spatial scales necessarily overlap, and Schooley *et al.* (2000) discuss how one engineer operating at a larger scale affects another engineer affecting small-scale processes. In their desert system, kangaroo rats (*Dipodomys spectabilis*) are ecosystem engineers that build large mounds that influence the spatial distribution of fungi, plants, and some ground-dwelling animals. Many ant species and their more localized engineering influences on soil properties and redistribution of resources such as water and organic matter may respond to patch disturbances by kangaroo rats. This relationship generates a nested spatial hierarchy of animal engineering.

We suggest then that engineers can operate on spatial scales that include and exceed the scales of biotic interactions, but that the impacts of engineering will be most important and visible at large scales. Similarly, Mitsch & Day (2004) note that ecological feedbacks caused by organisms like ecosystem engineers are difficult if not impossible to be properly studied in small-scale experiments. Wright *et al.* (2003) claim that when species are dispersal limited, ecosystem engineers will have large effects by controlling the distribution and abundance of engineered patches in the landscape, which suggests that larger-scale studies will be more informative.

Time and space combined

Combining the consideration of spatial and temporal dynamics clearly demonstrates both the richness and complexity of engineering-induced changes to ecosystems. For example, engineering legacies imply differential environmental decay rates back to an unmodified state. When combined with the recognition that spatially mobile engineers can return to sites and re-engineer them, the resulting spatial and temporal dynamics at both small and large scales is likely to be quite complex.

Unfortunately, data on temporal and spatial scales in ecology are still far from complete, so we cannot give a complete overview of the importance of time and space scales, comparing ecosystem engineers and species whose biotic interactions predominate. However, we have compiled a list (Table 2) of ecosystem engineers and the temporal and spatial scales of their effects. Thus, the examples we have emphasized here on the importance of engineering based on its larger spatial and temporal extent are in fact found in a number of taxa and systems. The challenge is to properly incorporate these spatial and temporal scales into descriptions and predictions.

MODELS OF ECOSYSTEM ENGINEERS

Models played, and will continue to play, a fundamental role in developing the ecosystem engineering concept (Gurney & Lawton 1996; Klausmeier 1999; Laland *et al.* 1999; Odling-Smee *et al.* 2003; Cuddington & Hastings 2004; Wright *et al.* 2004). Future efforts will be most fruitful, however, if they account for the scaling issues raised above (Fig. 1 and Table 2). Essentially, engineer models differ from standard models by explicitly including the modification of the habitat by the engineer (as illustrated in Fig. 1) and the decay rate of the environment following modification (hence a potential time lag). If the physical aspects are on a different spatial scale, then that scale would need to be explicitly included as well. The examples listed in Table 2 provide a set of species for which these kinds of models could be

essential. The explicit inclusion of the physical 'box' (Fig. 1) contrasts with the implicit effect of species on their habitat through density dependence that is typically included in population-based models. Nevertheless, the fundamental issues that many models of engineers could address are essentially those of all populations and community ecologies – what determines the distribution and abundance of species? More specifically, the models highlight when specific inclusion of habitat creation and decay leads to different conclusions than when these effects are subsumed into biotic interactions.

The development of models of ecosystem engineers has encompassed the conceptual and general, and the system specific. General models include at least one species, and at least one variable for habitat. The first general mathematical model specific to ecosystem engineering was that of Gurney & Lawton (1996) who illustrated the importance of engineering for the persistence of a single species that cooperatively modifies its habitat. This model had a single variable for population size, and habitat (in a spatially implicit context) was described by a single variable measuring the proportion of the habitat in an engineered state vs. a virgin (unmodified) state. A notable aspect was the inclusion of explicit time delays in a variant of the basic model as a way to incorporate long-term effects of the engineers. The results demonstrate how (and when) engineering can be essential for survival of the engineer. Wright *et al.* (2004) extended this basic model to the landscape scale to encompass spatially implicit patch dynamics and how this affected and was affected by the engineer population, making the general model operational for a specific engineer, beaver.

In a similar vein, the use of spatially implicit models for engineers was extended by Cuddington & Hastings (2004) who focused on the dynamics of their model, rather than its equilibrium or long-term behaviour. In this model, the distribution of habitat quality along a gradient is considered using an integrodifference formulation, so the model begins with a more complete description of habitat state than Gurney & Lawton (1996). Although the model was developed in the context of the spatial spread of invasive species, it is essentially a conceptual one, as it is spatially implicit. In this model, the environment determined the spatial heterogeneity of the effects of the engineer species: it was assumed that large environmental flows would spread the impact of the engineer across a larger area, and consequently create smaller, more homogeneous changes. The model demonstrates that the rate of spatial spread of an invasive can be greatly accelerated by engineering, essentially concentrating on positive feedbacks in the dashed lines on the left of Fig. 1a. When viewed this way, the model has another implication not emphasized in the original article, namely that control efforts which only reduce the engin-

eer species and do not also focus on the engineered physical aspects can lead to different outcomes than efforts that focus on both the physical structures and the species. As engineers can improve suboptimal habitat, reinvasion by the same species could proceed at a faster rate than would be predicted if the physical changes, and their persistence after the death of the organisms, were not taken into account. In addition, impact of the engineered structure on other species would also persist, as further explored in Byers *et al.* (2006).

Another approach to the modelling of engineers includes more specific details of their engineering activities. Several specific models have focused on interactions between water and vegetation, illustrating the essential importance of the engineering concept for understanding the generation of spatial pattern and its subsequent dynamics (Klausmeier 1999; van de Koppel *et al.* 2002). One important difference here is that space is considered explicitly, with the goal of explaining the spatial distribution of vegetation. These models can be phrased in terms of integrodifferential equations and show how Turing type effects (reviewed in Levin 1992) arising from the interaction with the physical environment can generate spatial pattern.

The role of evolutionary forces in determining the niche of an ecosystem engineer has also received considerable attention (Laland *et al.* 1999). The implication is that ecosystem engineering is both affecting and affected by natural selection. The explicit use of a simple genetic two-locus niche-construction model shows that novel evolutionary dynamics can result from ecosystem engineering, with a key role played by temporal scales. As Laland *et al.* (1999) emphasize, one characteristic of niche construction (or equivalently ecosystem engineering) is to lengthen the ecological time scale, which means that the evolutionary and ecological processes are operating on more similar time scales. This then leads to much more complex dynamics (in time) because the time scales of ecology and evolution cannot be separated and therefore different kinds of feedbacks are possible. No doubt there is much more to learn from such a perspective on engineering, particularly the way engineers may affect the evolution of other species occupying engineered habitats.

As would be expected given the relatively recent development of the field, this brief review has shown that explicit mathematical models of ecosystem engineers are still rather primitive. However, it is clear that spatial and temporal scales have large impact on the model predictions. Important conclusions about general principles, such as the role of engineering for the persistence or spread of a single species have been drawn, but many important and obvious questions remain to be addressed. Although the heuristic development of the ecosystem engineering concept has focused on multiple species issues, formal mathematical

models still need to be extended to multiple species, to multiple engineers, to the potential importance of underlying abiotic environmental heterogeneity, and to temporal dynamics in complex spatial arrangements.

Perhaps most important for the continued development of models of ecosystem engineers is an appropriately balanced tension between general models and models that explicitly include a specific physical aspect of the environment as the focus. Not surprisingly, the existing models that have performed the latter have focused on the role of water in arid environments, a relatively straightforward, dominant driving variable. The explicit inclusion in models of other physical aspects with distinctive scaling features is an important area for future development.

CONTRIBUTIONS OF THE ECOSYSTEM ENGINEERING CONCEPT TO BASIC ECOLOGICAL THEORIES

In general, a scale-based emphasis on ecosystem engineering concept can inform ecological theories which seek to predict organismal or environmental dynamics that include the abiotic environment as either a stochastic or deterministic force. Here, we assess the potential contributions of ecosystem engineering to basic ecological theory organized along an ecological hierarchy from species to biomes.

Individuals and species

At the most basic level ecosystem engineering helps account for abiotic variability. Clearly, the physical and chemical environment is fundamentally important to organisms (Andrewartha & Birch 1954; Rice 1974) but is often highly variable in space and time, leading to ecological unpredictability, and in turn, to problems of predicting consequences (e.g. predicting effects of climate change on organisms). The engineering concept suggests that, in some cases, environmental variation may neither be entirely stochastic nor extrinsically determined, but an orderly and potentially predictable consequence of organismal activities. For example, organisms are often distributed across physical gradients according to their physiological tolerances, but occupancy of otherwise intolerable areas can occur when abiotic stress is ameliorated by other species (e.g. facilitation; Bruno *et al.* 2003; Crain & Bertness 2006). Active modification of the environment at larger scales can also occur through engineering, similarly resulting in high-density occupation of suboptimal areas over time (Cuddington & Hastings 2004).

Engineering activities can provide refugia from or increase exposure to abiotic forcing and predation, all of which can affect species life-history characteristics, such as reproductive size or age, mobility, mate selection traits,

degree of specialization or competitive ability (Grime 1977). More recently, authors focusing on niche construction (Odling-Smee *et al.* 2003) have shown how ecosystem engineering increases the interplay between ecology and evolution by putting these two aspects on a similar temporal scale.

Populations

Engineering can help us understand the mechanisms underlying and consequences of density dependence. Because ecosystem engineering can create cycles of habitat degradation and rehabilitation, it can affect population cycles of the engineer (if present in the system) and/or, in turn, the population cycles of organisms responding to the engineered environmental changes (Gurney & Lawton 1996). Engineering may also offer explanations for overshoots or drops in population levels; the effects of an engineer, especially when external to the system and not experiencing feedbacks (i.e. accidental, Jones *et al.* 1994), may directly contribute to fluctuations, or do so in concert with environmentally stochastic events.

The effects of engineering may be especially important in explaining the higher diversity in biogeographical transition zones where engineering may cumulatively increase spatial heterogeneity (Wright & Jones 2006) such that more species can persist in these relatively small areas (small relative to the rest of the species' ranges). Engineering may also help explain the success of species invasions; engineers may make novel habitat suitable for themselves, altering the environment for incumbent species while enhancing conditions for their spread (Cuddington & Hastings 2004).

Engineering may influence the genetic diversity of populations of both the engineer and associated species through feedbacks that result in changes in spatial heterogeneity, habitat area, habitat quality or connectivity between populations (Laland *et al.* 1999; Wright *et al.* 2004; Wright & Jones 2006). For example, engineering can affect the extinction and (re)colonization rates of habitat patches, which is known to influence genetic diversity of fragmented populations in complex ways (McCauley 1993).

The ecosystem engineering concept helps afford general explanation for patch conditions (e.g. engineered vs. unengineered), patch formation and maintenance, the abiotically influenced dynamics of organisms within patches, the population dynamics of the engineers, and links to the patches they create across the landscape (Wright *et al.* 2004).

Communities

Many of the documented community-level effects of engineers may be related to the alteration of habitat heterogeneity at patch and landscape scales. Locally,

engineers may either increase or decrease patch-level diversity, most likely by changing habitat complexity (Crooks 2002). At larger spatial scales, species diversity in a landscape of engineered and unmodified patches is likely to be increased, given differing habitat requirements of species responding to engineered and unengineered spaces (Jones *et al.* 1997; Wright *et al.* 2002; Wright & Jones 2004). Similarly, engineers can increase environmental heterogeneity by altering habitat structure and distributions of resources, as in the simple one-species (tiger brush) system modelled by Klausmeier (1999). The direction of engineering–diversity relationships will depend both on scale and the life history of the species involved. For example, the invasion of a marine mussel added small-scale structure and increased fine-scale diversity for surface-dwelling organisms, while the diversity of larger, subsurface-dwelling organisms declined (Crooks 2002). In a similar way, engineering can contribute to theories of species coexistence. If engineers create different environments, and if species can sort themselves out along these environments and adapt to them, then engineering should markedly enhance opportunities for niche differentiation, diversification and coexistence at the same or multiple trophic levels (Laland *et al.* 1999; Erwin 2005; Crain & Bertness 2006).

Engineering can affect food webs and our interpretation of trophic interactions in two basic ways. First, engineering may affect the spatial heterogeneity that is important in the organization of food webs (e.g. resource distribution patterns). Second, food webs narrate only part of the story of interactions among species and their environment as all organisms engage in both trophic and engineering interactions to some degree (Wilby *et al.* 2001). The relative importance of trophic and engineering activities in an ecosystem is contingent on the species, environmental conditions and time scales. Determining the conditions under which engineering results in stronger interactions than trophic effects may explain observed anomalies in species distributions attributed to trophic interactions and may increase our ability to predict community change.

Both succession and community assembly are common ecological theories underlying ecosystem restoration (Young *et al.* 2001). Often, unexpected restoration outcomes illustrate that such theories lack predictive power. Both theories focus on community outcomes with little explicit consideration of biotic–abiotic relationships and structural processes, both of which are explicit in the engineering concept. Succession theory and the emerging recognition of the importance of facilitation in this process does acknowledge these relationships (Bruno *et al.* 2003; Crain & Bertness 2006), and the kinds of scale issues we raise here in terms of engineering should enhance this approach.

Ecosystems

Ecosystem engineering makes explicit a particular form of influence on energy and nutrient flows within and between ecosystems. Like all species, engineers have assimilatory and dissimilatory roles in the ecosystem that contribute to energy flow and nutrient cycling. However, their engineering activities act as controls on such flows largely because the abiotic environment is a master influence on such processes. As a consequence they often affect biogeochemical process rates and distributions (e.g. Gutiérrez and Jones 2006), and can play a major role in the input or export of materials from ecosystems (e.g. Gutiérrez *et al.* 2006) thereby having effects at larger spatial scales. Similarly, as other organisms within the ecosystem may be affected by the engineering, this can also alter their roles in energy and nutrient flows (Jones *et al.* 1997).

Across ecosystems, connectivity depends upon the permeability of boundaries or corridors between systems (Talley *et al.* 2006), and it is here that the potentially larger spatial scale influence of ecosystem engineers may come into play (Fig. 1 and Table 2). Engineering may enhance or inhibit this connectivity through activities at the boundary or within the transition zone or corridor, such as creating refugia from predators or stress or, conversely, providing habitat for predators and increasing stress or disturbance. Engineering activities occurring within one of the adjacent ecosystems or outside of the system altogether may also influence connectivity by modulating cross-system flows of energy, material or information (i.e. allochthonous inputs, see ecosystem level above). An obvious example of altered connectivity is the influence of beaver dams on downstream sediment flows.

At larger scales, the collective influence of populations or communities of engineers on the abiotic environment potentially contribute to regional or global climate change (Whitham *et al.* 2002). Such influences may arise from structural morphology or behaviours that result in habitat change. For example, regional forests such as the rainforests of Central and South America are comprised of many tree species that not only control local climate, but affect global climate through additions of moisture and volatile organic carbon emissions. Predictions of these global-scale processes, as well as small-scale ones, will benefit from explicit consideration of ecosystem engineers.

EXPERIMENTAL AND OBSERVATIONAL APPROACHES TO ECOSYSTEM ENGINEERS

The explicit recognition of the role of temporal and spatial scales in ecosystem engineering highlights challenges for observational and experimental studies. In particular, explicit examination of physical processes and attention to

larger temporal and spatial scales is required. Conversely, a recognition of the central role of scale helps provide a framework for designing effective studies.

Ecosystem engineers and their consequences span the full breadth of ecology. Thus, a standardized approach to studying ecosystem engineers should allow comparisons across systems and tests of general hypotheses (Wright & Jones 2006). Fortunately, the ecosystem engineering concept also provides a clear organizational framework. One of the key insights is the clear distinction between engineering processes that describe the interaction between organisms and the abiotic environment, and the consequences of these processes for organisms (Jones *et al.* 1994, 1997; Wright & Jones 2006). In its complete form, ecosystem engineering studies involve two distinct but linked hypotheses: an organism influences a set of target abiotic variables through altered structure or chemical reactivity, and these altered abiotic variables then influence a set of target biological traits.

Physical ecosystem engineers exert their influence on the abiotic environment through the creation (or destruction, modification and maintenance) of structure. Consequently, studies can ask questions about three distinct components of the ecosystem engineering process: (i) how does engineer abundance and type of physical activity influence the form, spatial distribution and temporal persistence of structural change? (ii) How do physical processes then influence the persistence of structure and its effects in the landscape? (iii) How does structural change influence the target abiotic variables? A fundamental method for testing ecological interactions is to manipulate the presence or abundance of one species and measure the response in a set of target species. The ecosystem engineering framework makes explicit that such experiments by themselves do not test underlying mechanistic processes. Answers to the above questions then inform our expectations about engineering consequence for the engineer and other species, i.e. how do changes in the target abiotic variables influence the target biotic variables?

Each of these components can be studied separately or together as integrated units depending on motivation. For instance, Arens *et al.* (2001) investigated how vegetation moderates sand erosion to better predict the profile development of dunes, but this work did not test the consequence of this modification for the dune biota. Many questions, however, require explicit tests of the dynamic links between components. For example, primary production by the salt marsh dominant *Spartina alterniflora* causes significant sediment accumulation and increased tidal elevation. To test the potential consequence of sea level rise in this system, Morris *et al.* (2002) quantified both the influence of *S. alterniflora* production on elevation and the influence of elevation on *S. alterniflora* production.

Besides engineering, species engage in numerous other interactions such as direct resource competition and trophic relationships. A clear future direction for ecosystem engineering studies is to quantify the role of ecosystem engineering relative to these other processes (e.g. Wilby *et al.* 2001), which as emphasized in Fig. 1 and Table 2, often involves investigations on multiple temporal and spatial scales. One promising method for decomposing such species interactions is the use of structural mimics coupled with traditional removal experiments (Crooks 2002). In addition, the interaction between ecosystem engineering, other species interactions and external abiotic forcing likely has important consequences for community dynamics. For instance, bush lupines (*Lupinus arboreus*) in coastal California provide patchy microclimate refuges for an entomopathogenic nematode (*Heterorhabditis marelatus*), an important predator of the lupine feeding ghost moth (*Hepialus californicus*). In typical years, the poorly dispersing nematodes are restricted to relatively few lupine refuges, and outbreaks of the ghost moth are common. During wet El Niño years, however, nematode survival and consequent suppression of the ghost moth significantly increases (Preisser & Strong 2004). Documenting how processes such as trophic interactions both create and are influenced by the spatial and temporal heterogeneity of engineered habitat is an important area of future research. In addition, more studies are needed that document how external variation in the abiotic environment influences such interactions. Another important question is the degree to which ecosystem engineering effects vary across environmental gradients (Crain & Bertness 2006). A challenge for such studies is to define common metrics and scaling principles that will allow general comparisons across systems and classes of ecosystem engineers (Wright & Jones 2006).

APPLICATIONS OF THE ENGINEERING CONCEPT

The engineering concept has a number of implications for applied ecology. These can be considered both in terms of assessing the benefits and costs of engineers as well as providing guidance for harnessing the power of nature's engineers to do desired environmental work. In the broadest sense, the work of ecosystem engineers offers models and lessons for the way in which humans engineer the environment (Jones *et al.* 1994), such as modifying hydrology (Rosemond & Anderson 2003). Ecosystem engineers also provide ecosystem services, such as environmental buffering and regulating soils, water and climate. The engineering concept, however, has yet to be explicitly incorporated into consideration of ecosystem services (e.g. Kremen 2005). In addition, engineers can be focal elements of applied efforts involving conservation of species and habitats, invasive species management and restoration (Byers *et al.* 2006; Wright & Jones 2006).

The loss of ecosystem engineers from systems represents a major conservation concern, as the alteration of the abiotic realm by engineers often has wide ranging, cascading consequences for other biota (Coleman & Williams 2002). Engineers can thus typify the type of 'strongly interacting species' that constitute conservation targets (Soulé *et al.* 2005 and references therein). Some engineer species of conservation interest play roles in maintaining or protecting habitats, such as prairie dogs which rework soils, and vegetation that prevents soil erosion. Other engineers define the habitat itself, such as forest-producing trees and reef-building corals, and protection of such species and the habitats they create is at the forefront of global conservation efforts.

Adding engineers to systems can also have profound consequences, as made clear by many high profile invasions of some exotic species into ecosystems (Crooks 2002 and references therein). The invasion of exotic trees into unvegetated areas creates forests where none existed before, while browsing by introduced herbivores has the opposite effect. Some other effects of exotic engineers include tamarisk changing water tables, filter-feeding zebra mussels creating hard substrates for attachment and increasing water clarity and light for the algae they feed on, bioeroding crustaceans destroying salt marshes and mangrove forests, and grasses changing fire regimes. Understanding the role of engineering in biological invasions is important in that it can help place all these seemingly disparate effects into a common framework, and highlights the need to consider the breadth of interactions of invaders with resident species (thus avoiding potential pitfalls of only focusing on, e.g. competitive effects). Applying the engineering concept also can increase our understanding of the dynamics of invasion, such as through the feedback between habitat alteration and rate of spread (Cuddington & Hastings 2004). In the context of invasive species management, recognition of engineering suggests that these habitat modifiers would be important species to target for control as long as the cascading effects of their removal, including long-lasting environmental legacies, are considered (Byers *et al.* 2002).

A better understanding of ecosystem engineers and the functions they perform also can help us deliberately use ecosystem engineers to do work for us. In restoration ecology, there has been an increased emphasis on 'bottom-up' approaches and 'directing ecological succession' (D'Antonio *et al.* 2004), such as using 'nurse plants' which moderate local environmental conditions (Padilla & Pugnaire 2006). Ecosystem engineering can inform these efforts, and can more broadly provide conceptual underpinnings for restoration as a whole. For example, a framework has recently been developed which considers restoration in the context of two stable states influenced by abiotic and biotic factors, and demonstrates how efforts

could most effectively be partitioned between direct human intervention and utilizing ecosystem engineers (Byers *et al.* 2006). Employing the functions of engineers also can be of value in efforts such as bioremediation, landscaping, and urban planning. Even human health and well-being can depend on ecosystem engineers, as made clear by the devastating effects of recent natural disasters (tsunamis and hurricanes) and the role of coastal vegetation and lack thereof in protection from wave and wind damage (e.g. Danielsen *et al.* 2005).

FUTURE DIRECTIONS AND CONCLUSIONS

Our review has shown how the ecosystem engineering concept can contribute to a better understanding of the functioning of ecosystems in both basic and applied realms. We have emphasized that the concept is fundamentally intertwined with the issues of spatial, temporal, and organizational scale that are central to contemporary ecology.

Essentially all species interact to some extent with other species through the physical environment, but clearly the extent of this interaction and its consequence varies from species to species and depends on environmental context. Species affect other species in a range of ways and on a continuum from biotic interactions, which may be direct or indirect, to abiotically mediated interactions, which must be indirect. Ecosystem engineering represents the latter end of this continuum, and explicit recognition of the engineering aspect helps us address both applied and basic questions. Thus, studying ecosystem engineering is an essential part of the growing emphasis in ecology on explicit inclusion of time and space (Levin 1992).

What is somewhat surprising is that explicit mathematical models of ecosystem engineers and engineering are still quite limited, and much more work is needed here. Although it is clear from the current single species and evolutionary models that engineering effects can both be important and different from biotic interactions (see Fig. 1), essentially no detailed models have gone beyond the single species. More complex multispecies models explicitly including time and space scales would certainly be needed to apply the concepts developed here in the applied realm, and in this context, the ecosystem engineering concept will prove particularly useful (e.g. Byers *et al.* 2006).

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